Forest Ecology and Management 328 (2014) 262–269

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

3D dental microwear texture analysis of feeding habits of sympatric ruminants in the Białowieża Primeval Forest, Poland

Gildas Merceron [a,*], Emilia Hofman-Kamińska [b], Rafał Kowalczyk [b]

[a] iPHEP, UMR 7262, CNRS & University of Poitiers, France
[b] Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland

ARTICLE INFO

Article history:
Received 18 December 2013
Received in revised form 23 May 2014
Accepted 24 May 2014
Available online 22 June 2014

Keyword:
Bison bonasus
Cervus elaphus
Capreolus capreolus
Alces alces
Diet
Food niche overlap

ABSTRACT

With four species of ruminants, including red deer, roe deer, moose, and European bison, the Białowieża Primeval Forest is unique on the European continent, where only one to three ungulate species are usually found. The present study is the first effort to explore the dietary overlap of a European community of sympatric ruminants using 3D dental microwear texture analysis. Results obtained for ungulates from the Białowieża Forest were compared with those of four species with well known differences in diet (semi-wild Heck cattle, African buffaloes, giraffes, and yellow-backed duikers). These ruminants frame the spectrum of expected 3D dental microwear textures among ruminants: C3 and C4 grazers share high anisotropy and low to intermediate complexity while browsers display intermediate to high complexity associated with low anisotropy. No significant differences between browsers (moose and roe deer) and mixed feeders (red deer) were detected by this analysis supporting a significant overlap in diet found in Białowieża. The results on the fourth ruminant are unequivocal: the European bison is not grazer but instead is highly engaged in browsing. Furthermore, through 3D dental microwear texture analysis, the high plasticity in feeding behavior of the European bison can be tracked depending on the seasons and on available access to feeding supplements during the winter.

1. Introduction

Evidence of overlap in resource use by sympatric species is essential for the understanding of interspecific competition (Mysterud, 2000). Often, resource use by one species reduces availability of resources for another species or leads to species displacement (Putman, 1996; Ferretti et al., 2008). Competition for resource exploitation is one of the main mechanisms for interaction among large ungulates. Such interaction may occur when ungulates share similar habitats, an overlap in food consumed and when resources are limited (Gordon and Illius, 1989; Mysterud, 2000). Evidence of interactions among ungulates and other groups of species in natural ecosystems is limited (Putman, 1996).

The Białowieża Primeval Forest, located on the Polish-Belarussian border is one of the best preserved forests in Europe (Jędrzejewska and Jędrzejewski, 1998). With five species of ungulates (including red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, moose *Alces alces*, European bison *Bison bonasus* and wild boar *Sus scrofa*), it is unique on the European continent, largely inhabited by only one to three ungulate species (Okarma, 1995). Ungulates coexist here with a high diversity of carnivores, including wolves and lynx. These predators hunt roe and red deer almost exclusively (Jędrzejewska et al., 1997; Jędrzejewska and Jędrzejewski, 1998). Deciduous and mixed forests with rich undergrowth and herb layers offer good conditions for ungulates and may limit possible competition among them. In historical times, high densities of ungulates maintained for hunting purposes, together with cattle grazing in the forest (Samojlik and Kuijper, 2013), had a strong impact on tree stands and resulted in species competition. The two largest herbivores, the bison and the moose, were especially shaped by intra- and inter-specific competition for food resources (Jędrzejewska et al., 1997; Jędrzejewska and Jędrzejewski, 1998). Nowadays, populations of ungulates in Białowieża occur in moderate densities and their numbers are increasing (Borowik et al., 2013; Kowalczyk et al., 2013).

Cervids and European bison – the only bovidae species in the Białowieża Forest – are characterized by different feeding habits (Hoffman, 1989). The moose (*A. alces*) is the largest cervid. Its diet is mainly based on browsing trees and shrubs (birches, willows, rowan etc.) and herbaceous dicots; grasses and sedges being very rare in this diet (Morow, 1976; Franzmann, 1981). The red deer occupies various habitats from forest to moorland. In Europe, its

* Corresponding author. Tel.: +33 (0)5 49 36 63 05.
E-mail address: gildas.merceron@univ-poitiers.fr (G. Merceron).

http://dx.doi.org/10.1016/j.foreco.2014.05.041
0378-1127/

diet includes different proportions of browse and grass depending on the season, region and habitat (Gebert and Verheyden-Tixier, 2001). Roe deer - the most widely distributed European ungulate species (Linnell et al., 1998) – is recognized as being a selective feeder (browser) occupying a large set of habitats from open cultivated areas to dense forest (Tixier and Duncan, 1996). The European bison, the largest terrestrial mammal in Europe, restored from captive survivors following its extinction in the wild at the beginning of the 20th century, is found mainly in forest habitats (Krasińska and Krasiński, 2007; Kerley et al., 2012). It is assumed to be a mixed feeder or grazer (Hoffman, 1989; Krasińska and Krasiński, 2007; Kowalczyk et al., 2011), however its diet differs strongly from summer to winter due to the supplementary feeding widely used for the management of species conservation (Kerley et al., 2012). In the last two decades, however, agricultural land providing crops of rapeseed and cereals or hay left by farmers in the meadows has been more frequently used in winter and some seasonal migrations can therefore be observed (Kowalczyk et al., 2011; Hofman-Kamińska and Kowalczyk, 2012).

In the present study, we explore the dietary preferences of the four sympatric ruminants from the Białowieża Forest through 3D dental microwear texture analysis (3D-DMTA). The 3D-DMTA is based on the automated quantification of 3D surfaces by using a scale-sensitive fractal analysis. It has proved to be very efficient in discriminating dietary differences between species of primates both extant and extinct (Merceron et al., 2009; Ungar et al., 2010; Scott et al., 2012) as well as ungulates (Ungar et al., 2007; Scott, 2012) and carnivores (DeSantis et al., 2012; Stynder et al., 2012). Because it only provides information for a timescale ranging from a few days to a few weeks (Teaford and Oyen, 1989; Schulz et al., 2013), the dental microwear texture is an appropriate proxy to detect seasonal variations in diet and to pinpoint the exploitation of fallback foods (Merceron et al., 2010), i.e. food items that are consumed when preferred food is not available anymore. Through this 3D dental microwear texture analysis, we will explore the resource partitioning or overlapping among the four sympatric ruminants.

We aimed to: (i) establish a first comparative dataset of wild European ungulates for 3D-DMTA, (ii) explore the ecological niche partitioning among a guild of wild and sympatric ungulates including bovids and cervids inhabiting the very same area, and (iii) and then assess the foraging habits of European bison recognized recently as a refugee species in European forests (Kerley et al., 2012). More specifically, we aim to assess the portion of abrasive grasses in the bison's diet all year round, notably in winter when certain bison herds have access to supplementary hay fodder. Thus, results of this study might have implications for future management strategies for European bison conservation.

2. Material and methods

2.1. Material

2.1.1. The Białowieża forest

This study was conducted in the Polish part of the Białowieża Primeval Forest (52°35′–52°55′N, 23°30′–24°00′E; 625 km^2), one of the best preserved temperate lowland forests in Europe. The dominating habitats found there are mixed coniferous and mixed deciduous forest (pine *Pinus silvestris*, spruce *Picea abies*, oak *Quercus robur*, with admixtures of birch *Betula* spp., and aspen *Populus tremula*), which covers 39.3% of the area and rich deciduous forest (oak *Q. robur*, hornbeam *Carpinus betulus*, lime *Tilia cordata*, and maple *Acer platanoides*) covering 34.9%. Wet alder-ash forest (black alder *Alnus glutinosa*, ash *Fraxinus excelsior*) covers 12.6% of the area, coniferous forest (mainly pine *P. silvestris*, and spruce *P. abies)* covers 6.2%, and open habitats within the forest cover 7% (Sokołowski, 2004). Most of habitats are covered with rich undergrowth dominated by hornbeam (37%) and Norway spruce (22%) (Podgórski et al., 2008; Kowalczyk et al., 2011). The Forest is surrounded by agricultural areas with meadows, wastelands and arable land interspersed with small woodlands. The study area included both Białowieża National Park (17%) and the exploited forests (83%, of which 34% is protected). The latter are exploited by clear cutting small areas for natural regeneration or replanting.

The climate of Białowieża Primeval Forest is transitional, between the Atlantic and continental types, with clearly marked cold and warm seasons. The average annual temperature is 7 °C. The coldest month is January (average daily temperature is −4.8 °C), and the warmest is July (18.4 °C). Snow cover persists for 60–96 days per year with a maximum recorded depth of 95 cm (Jędrzejewska and Jędrzejewski, 1998).

The densities of the four species of ruminants are as follows: European bison −0.7 individual per km^2, red deer (*C. elaphus*) −6.0 individual per km^2, roe deer (*C. capreolus*) −2.0 individual per km^2 and moose (*A. alces*) −0.08 individual per km^2. As well as this, the density of wild boar (*S. scrofa*) reaches 5.4 individual per km^2 (Borowik et al., 2013).

2.1.2. The Białowieża ruminants

3D dental microwear texture analysis is applied on 86 specimens of ruminants from the Białowieża Forest, including 19 roe deer, 14 red deer, 8 moose, and 45 European bison. All specimens were living free before being culled or found dead in the Białowieża Forest and their skulls are stored in the mammal collection of the Mammal Research Institute, Białowieża (Poland). For most of them, date of death and gender are known. All moose and roe deer were culled in winter. The red deer sample is more heterogeneous including individuals shot in winter and spring, and 6 individuals over 14 red deer for which date of death is unknown. However, they were shot during the hunting period in fall and winter (Appendix 1).

Among the 45 individuals of European bison, 39 can be clustered in four groups defined by period of death and access to supplementary hay fodder in winter (Table 1). The first group of bison (Bison #1; $N = 18$) is composed of individuals sampled from spring to summer (from April to September). During that span of time, the understory vegetation in the primary forest of Białowieża offers abundant resources for bison (Faliński, 1986; Jędrzejewska et al., 1997). The groups Bison #2 ($N = 8$), Bison #3 ($N = 7$), and Bison #4 ($N = 6$) consist of individuals sampled in late autumn and winter (from November to early March; Table 1). Bison #2 group is composed of individuals from populations intensively fed with hay (3–5 times a week); Bison #3 with individuals less intensively fed with hay (usually once a week). Non-fed individuals using mainly agricultural areas in winter compose the fourth group (Bison #4; Table 1; see also Kowalczyk et al., 2011). The rest of the bison sample (6 individuals) were sampled in October. We made the choice to exclude them from the intra-population analysis in order to keep samples with sharp differences in vegetal resources access (see Appendix 1).

2.1.3. A comparative dataset

Our analysis includes 58 individuals representing four species of ruminants with clearly defined and well known differences in diet to serve as reference points and frame the spectrum of expected 3D dental microwear textures among ruminants (Table 1). The African buffaloes (*Syncerus caffer*; $N = 8$) from open landscapes in Central and Eastern Africa and the semi-wild, non-fed Heck cattle (*Bos taurus*; $N = 8$) from Oostvaardersplassen (Netherlands) are grazers; the former mostly foraging on C_4 and the latter on C_3 monocotyledonous (Sinclair, 1977; Estes, 1991;